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FOOD AND FEEDING OF SPERM WHALES *PHYSETER MACROCEPHALUS* OFF THE WEST COAST OF SOUTH AFRICA

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The stomach contents of 1 268 sperm whales *Physeter macrocephalus* processed at the Donkergat whaling station, South Africa, were examined during the 1962 and 1963 whaling seasons. Results were compared with Clarke's analysis of cephalopod beaks collected in 1963 (Clarke 1980). There was no significant difference in the incidence of food in the stomachs between whales taken in the morning (07:15–11:15), at midday (11:15–15:15) or in the afternoon (after 15:15). The incidence of food remains was less in medium-sized (12.2–13.7 m) and large (≥14 m) males than in small (≤11.9 m) males and females, and their stomachs more frequently contained the beaks of cephalopod species from the Antarctic or subAntarctic. These phenomena were related to a winter migration of medium-sized and large males into the whaling ground from south of the Subtropical Convergence. Medium-sized and large males fed more frequently on larger species of endemic cephalopods than females or small males, whereas males in general ate larger individuals of a cephalopod species than females. Because larger and older individuals within a cephalopod species are frequently distributed deeper than other individuals, males may feed lower in the water column than females. Evidence from catch positions and the incidence of non-cephalopod prey items suggests that some males within the West Coast whaling ground moved into the continental slope water (200–1 000 m deep), where they dived to the sea floor and took benthic organisms such as rajids, crabs, *Lophius* sp. and *Allocyttus* sp. Females stayed farther offshore, where both sexes fed mesopelagically, consuming mesopelagic-bathypelagic cephalopods, *Ruvettus* sp., mysids and ceratids. Some of the differences in distribution and feeding behaviour between males and females may reflect adaptations to the social organization of the species.

"*And what thing soever besides cometh within the chaos of this monster's mouth, be it beast, boat or stone, down it goes all incontinently that foul great swallow of his, and perisheth in the bottomless gulf of his paunch*".

Holland's Plutarch's Morals in *Moby Dick or The Whale*. Melville, H. 1851. New York, Harper Bros.

Sperm whales *Physeter macrocephalus* are the largest of the toothed whales, the most sexually dimorphic in size, and among the deepest divers. Reaching depths of at least 1 134 m (Heezen 1957) and possibly up to 2 000–2 250 m (Norris and Harvey 1972, Watkins *et al*. 1993) and remaining submerged for up to 82 minutes (Clarke 1976) and possibly 128 minutes (Watkins *et al*. 1985), sperm whales are able to sample the mesopelagic and bathypelagic cephalopod fauna much more effectively than most commercial squid fisheries or research trawls (Clarke 1977). In addition, the species is recorded as taking a wide variety of deep-sea fish and other organisms (Kawamura 1980), for which there is often little information in the area concerned. Consequently, the stomach contents of sperm whales are a potential source of information on the occurrence of poorly known mesopelagic and bathypelagic organisms. Conversely, what knowledge there is of the biology of their prey can assist in the interpretation of sperm whale feeding behaviour (Clarke 1980).

In this paper, data on the food and feeding behaviour of sperm whales on the west coast of South Africa are presented, based on the examination of animals processed at the former land station at Donkergat, Saldanha Bay (33°05´S, 18°00´E), during the 1962 and 1963 whaling seasons. Despite the length of time since these data were collected, there has been no full account of sperm whale feeding behaviour in that region, although information from a collection of squid beaks and some squid specimen material originating from the Donkergat studies has already been published (Clarke 1980). As the whaling station closed in 1967, and the opportunity to examine such a large sample is unlikely to recur in the foreseeable future, this paper is an attempt at a summary of what is known about the extent and nature of sperm whale feeding in the region. Besides a review of the published data for cephalopods, the paper includes information on the incidence of food remains in the stomachs, and a description and analysis of the non-cephalopod prey items.

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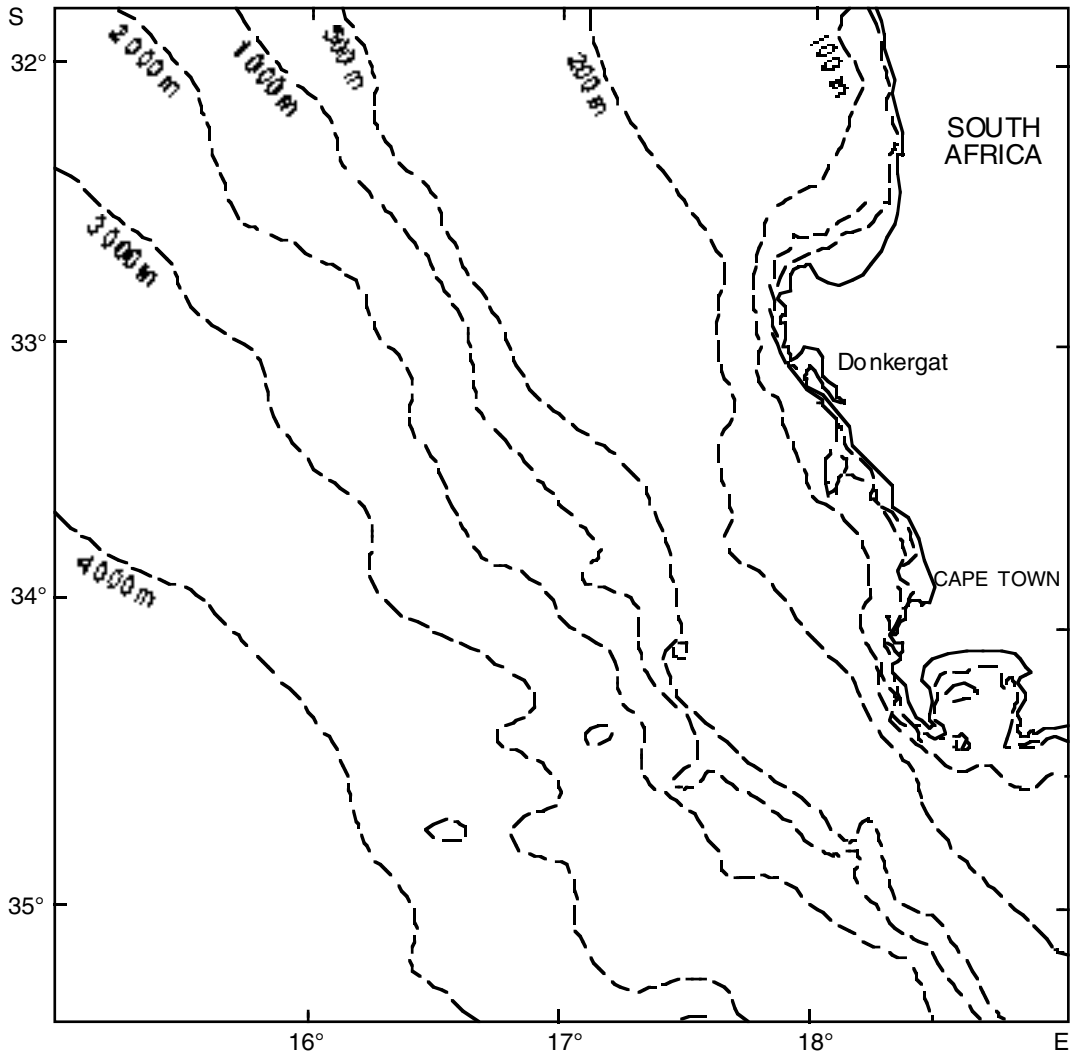

Fig. 1: Bathymetry of the West Coast whaling ground, South Africa

MATERIAL AND METHODS

Between 28 July and 1 November 1962, and from 2 March to 30 October 1963, a total of 1 271 sperm whales was landed at the Donkergat whaling station, Saldanha Bay (Fig. 1), of which 1 268 were examined systematically by the author.

The examinations usually included opening and inspecting the contents of the first and/or second stomach, if it had not suffered harpoon damage during capture. Because of time limitations, it was usually impossible to do more than make an incision through the stomach wall and examine the contents either as they spilled out on the deck, or were scooped/pulled by hand out of the stomach. Occasionally, when time allowed, a more thorough examination of the stomach would be made and mass/volumes measured. The contents were classified to type (squid, fish, crabs, mysids, tunicates, etc.) and individual prey items were counted. Numbers were based on mantles (cephalopods), skulls (fish), carapaces (crustaceans) or whole/

Table I: List of squid collected at Donkergat (1962 – 1963) from sperm whale stomachs, their code names and eventual identifications (from Clarke 1980)

Whale number	Date	Code name	Species
16	29 Jul. 1962	Chequered	*Pholidoteuthis boschmai*
176	18 Aug. 1962	Tiny (small)	*Octopoteuthis rugosa*
318	7 Sep. 1962	Dumpy	*Ancistrocheirus lesueuri*
328	13 Sep. 1962	Purple small fin	*Histioteuthis miranda*
329	13 Sep. 1962	Spotted heart fin	*Moroteuthis robsoni*
331	13 Sep. 1962	Spotted heart fin	*Moroteuthis robsoni*
651	13 Oct. 1962	Long white thin	*Moroteuthis robsoni*
802	2 Nov. 1962	Tiny (small)	*Octopoteuthis rugosa*
811	2 Nov. 1962	Chequered (×2)	*Pholidoteuthis boschmai* (×2)
811	2 Nov. 1962	Spotted small fin	*Moroteuthis robsoni*
-	7 Aug. 1962	Chequered	*Pholidoteuthis boschmai*
-	1962	*Architeuthis*	*Architeuthis* sp.
1033	7 Mar. 1963	Histioteuthid	*Histioteuthis bonnellii*
1080	22 Mar. 1963	Chequered	*Pholidoteuthis boschmai*
1081a	22 Mar. 1963	Histioteuthid	*Histioteuthis bonnellii*
1081b	22 Mar. 1963	Purple small fin	*Histioteuthis miranda*
1082	22 Mar. 1963	Large fin, bugle-shaped body, large head	*Cycloteuthis akimushkini*
1083	22 Mar. 1963	Histioteuthid	*Histioteuthis bonnellii*
1245	25 Apr. 1963	Large tiny, Cucioteuthid	*Taningia danae*
1249	25 Apr. 1963	*Architeuthis*	*Architeuthis* sp.
1889	18 Aug. 1963	Long thin	*Moroteuthis robsoni*
2336	29 Sep. 1963	Tiny (×2)	*Octopoteuthis rugosa* (×2)
2649	23 Oct. 1963	Dumpy	*Ancistrocheirus lesueuri*
2707	30 Oct. 1963	Scaly	*Lepidoteuthis grimaldii**

* Not identified by Clarke (1980), but determined from characteristic mantle scales

partial animals (tunicates). If only fragments (vertebrae, legs, tail segments, etc.) were present, the number of prey items was taken as one. Some indication as to state of digestion was also given, e.g.:

(i) whole squid, fresh (some pigmented skin left on mantle);
(ii) whole squid, digested (no skin left);
(iii) digested squid (mantles and buccal masses separate, remains in "soup");
(iv) squid beaks only.

If time permitted, the mantle lengths of some of the whole fresh squid were measured (with a ruler) to the nearest centimetre.

Because the author was not competent in cephalopod identification, and because the "heads" (tentacular masses) of most of the squid present in the stomachs had become separated from the mantles, reliance was placed on classifying the squid encountered into "types", based principally on the shape, colouration and texture of the mantle and fin. These were given convenient code names, and where reasonably intact squid in good condition were found, they were preserved in 5% formalin/seawater solution. Those that could be reliably identified (Clarke 1980) are listed in Table I.

Samples of cephalopod beaks were taken from individual stomachs as several handfuls (up to one bucketful) at random and without any sorting: such samples were collected from 38 animals in 1962 and 90 animals in 1963, and also preserved in 5% formalin. Information from the whole squid material and the 1963 beak collection (representing some 51 700 individual cephalopods) has already been published (Clarke 1980). In analyses of species composition by mass, it has been assumed that females and males of all sizes fed on similar-sized squid of each species, and the mean masses listed by Clarke for squid eaten by all sperm whales landed at Donkergat (his Table X) have been used accordingly.

The nomenclature used to describe cephalopod taxa in Clarke (1980) has been updated in this paper where necessary (see details in Clarke and Roeleveld 1998).

Contents of the first and second stomachs rarely differed as regards the nature of their contents or state of digestion, and (apart from the estimates of quantities eaten) all analyses in the paper have ignored whether the first or second stomach was examined.

In 1962, the stomach contents of 12 whales in reasonably fresh condition were weighed and their volumes measured, using a spring balance and a 9-ℓ steel bucket.

Results for male sperm whales have been expressed for three size-classes, originally measured to the nearest foot (0.31 m), but here expressed as metric equivalents: small (≤11.9 m), medium (12.2–13.7 m) and large (≥14.0 m), corresponding to recognized social

Table II: Incidence of food in sperm whales at Donkergat, 1962 – 1963

Season	Whole, fresh		Whole, digested		Digested		Beaks + empty		Total
	n	%	*n*	%	*n*	%	*n*	%	*n*
				Small males					
Autumn	26	17.7	45	30.6	39	26.5	37	25.2	147
Winter	9	5.8	47	30.3	44	28.4	55	35.5	155
Spring	28	10.3	91	33.3	71	26.0	83	30.4	273
Total	63	11.0	183	31.8	154	26.8	175	30.4	575
				Medium-sized males					
Autumn	4	5.1	17	21.8	16	20.5	41	52.6	78
Winter	1	4.8	8	38.1	8	38.1	4	19.0	21
Spring	8	10.4	30	39.0	10	13.0	29	37.7	77
Total	13	7.4	55	31.3	34	19.3	74	42.0	176
				Large males					
Autumn	0	0	3	17.6	6	35.3	8	47.1	17
Winter	0	0	0	0	3	42.9	4	57.1	7
Spring	0	0	5	33.3	5	33.3	5	33.3	15
Total	0	0	8	20.5	14	35.9	17	43.6	39
				Females					
Autumn	13	13.8	45	47.9	18	19.1	18	19.1	94
Winter	14	9.8	38	26.6	38	26.6	53	37.1	143
Spring	2	3.6	9	16.4	17	30.9	27	49.1	55
Total	29	9.9	92	31.5	73	25.0	98	33.6	292

groupings (Best 1979).

Seasonality in feeding was investigated by combining data for March–May (as autumn), June–August (as winter) and September–November (as spring).

The exact times at which whales were killed were not recorded, but the whale-catchers at Donkergat made radio contact with the station five times a day, at 07:15, 11:15, 15:15, 17:15 and 20:15, giving the numbers of whales killed on each occasion. As the tail of each whale was marked both with the catcher's identification number and the serial number of the whale killed that day, it was possible to assign a period during which the whale had been killed. For the purposes of analysing diurnal patterns of feeding behaviour, these periods have been defined as "morning" (07:15–11:15), "midday" (11:15–15:15) and "afternoon" (after 15:15) – no whales were taken before 07:15, and the very few whales taken after 17:15 have all been included in the "afternoon". Data suitable for this analysis were only collected from May to October 1963.

Catch positions were recorded as bearings and distances from the whaling station, and these have been converted to latitudes and longitudes. All animals taken from one school were allocated the same catch position (usually equivalent to the original sighting position, as relayed by the spotter aircraft or the first catcher to locate the whales). Because in reality the animals from a school were probably dispersed over a considerable distance (and in recognition of the limited accuracy of position-fixing in 1962 and 1963), catch positions were grouped by 12-minute (c. 22×18 km) cells of latitude and longitude for the purposes of analysis of distribution.

These squares were allocated to one of seven depth strata, depending on which stratum was dominant within the cell: 100–200, 200–500, 500–1 000, 1 000–2 000, 2 000–3 000, 3 000–4 000 and >4 000 m (Fig. 1).

RESULTS

Incidence of food

On the assumption that stomachs containing only squid beaks represented animals that have not fed for some time, they were combined with empty stomachs as representing non-feeding individuals. The frequency

Table III: Incidence of food against period of day when sperm whales were killed at Donkergat in 1963

Category of whale	Incidence of food	Morning (07:15–11:15)	Midday (11:15–15:15)	Afternoon (after 15:15)
Small males	Present	24	64	32
	Absent	13	49	23
	Total	37	113	55
Medium-sized + large males	Present	13	29	12
	Absent	12	10	2
	Total	25	39	14
Females	Present	27	48	45
	Absent	17	23	24
	Total	44	71	69

of occurrence of feeding individuals ranged from 56.4% in large males to 69.6% in small males (Table II) and was significantly different among small, medium and large males and females ($G = 4.61$, $p < 0.025$, $df = 3$). Subdividing the data indicates no significant difference in the frequency of occurrence of food in large males and medium-sized males ($G = 0.03$, $p > 0.75$, $df = 1$), nor in small males and females ($G = 0.87$, $p > 0.25$, $df = 1$), suggesting that medium-sized and large males fed less frequently than small males and females.

The frequency of occurrence of food in autumn, winter and spring (Table II) did not differ significantly in small males ($G = 3.80$, $p > 0.10$, $df = 2$) or large males ($G = 1.26$, $p > 0.50$, $df = 2$), but it did differ in medium-sized males ($G = 3.49$, $p < 0.025$, $df = 2$) and females ($G = 1\,198.60$, $p < 0.001$, $df = 2$). Subdividing the data suggests that the occurrence of food was higher in medium-sized males in winter, and lower in females in spring, than at other times of the year.

In investigating the diurnal pattern of feeding, data for medium-sized and large males were combined to increase the sample size (Table III). The frequency of occurrence of food in the stomachs did not differ significantly between morning, midday or afternoon periods, for either small males, medium-sized and large males combined, or females ($G = 0.79$, $p > 0.50$; $G = 5.79$, $p > 0.05$; $G = 0.46$, $p > 0.75$, respectively, each test with $df = 2$).

Quantity eaten

The contents of the stomachs of 12 whales were weighed and their volumes measured (Table IV). Quantities recorded ranged from 10.5 to 130.2 kg, representing 9.5–88 ℓ of squid. For the contents of five whales, the mean mass of the individual squid consumed ranged from 1.14 to 1.59 kg, whereas in two other cases the contents were dominated by a specimen of *Architeuthis* sp. In the last instances the squid weighed 21.6 and 82.3 kg respectively, indicating the potential importance of the species to the sperm whale's diet in the study area.

Table IV: Mass and volume of selected stomach contents of sperm whales at Donkergat in 1962

Date	Length (m)	Sex	Stomach	Mass (kg)	Volume (ℓ)	Contents
30 Jul. 1962	10.4	F	?	21.6	18.0	40% whole squid, 31.5% squid pieces, 28.5% beaks, pens, nematodes, etc. by mass
6 Sep. 1962	13.7	M	2nd	13.2	13.3	7 squid
6 Sep. 1962	13.4	M	2nd	18.6	16.1	13 squid (96.3% of total mass)
12 Sep. 1962	11.0	M	?	130.2	88.0	78 squid (95.4% of total mass)
12 Sep. 1962	11.3	M	?	24.5	17.5	16 squid (81.5% of total mass)
24 Sep. 1962	12.2	M	1st	10.5	9.5	4 squid
24 Sep. 1962	12.8	M	2nd	20.5	19.9	17 squid (incomplete contents)
25 Sep. 1962	10.7	M	1st	21.6	18.9	1 squid (*Architeuthis*?)
30 Sep. 1962	11.3	M	1st	63.9	55.8	30 squid (72.1% of total mass)
			2nd	20.0	16.4	3 squid (including one very large)
30 Sep. 1962	11.0	M	2nd	18.4	16.1	13 squid (80.2% of total mass)
10 Oct. 1962	10.7	M	1st	~46.6	~47.3	25 squid (only 5 weighed)
23 Oct. 1962	12.5	M	2nd	82.3	60.6	1 *Architeuthis* sp.

Table V: Incidence of principal food items in sperm whale stomachs at Donkergat, 1962 – 1963

Group	Number examined	Food item									
		Squid		Fish		Crabs		Mysids		Tunicates	
		n	%	*n*	%	*n*	%	*n*	%	*n*	%
Small males	584	400	68.5	47	8.0	7	1.2	34	5.8	44	7.5
Medium-sized males	168	102	60.7	19	11.3	3	1.8	4	2.4	15	8.9
Large males	41	22	53.7	2	4.9	2	4.9	2	4.9	4	9.8
Females	291	194	66.7	22	7.6	0	0	50	17.2	9	3.1
Total	1 084	718	66.2	90	8.3	12	1.1	90	8.3	72	6.6

Nature of food

By frequency of occurrence, squid (or cephalopods) dominated the stomach contents of both sexes and all size-classes (Table V). There was no significant difference in the frequency of occurrence of fish in stomachs of females, small, medium-sized or large males (G = 2.81, $p > 0.25$, $df = 3$). However, the occurrences of crabs, mysids and tunicates were statistically different between those groups of whales ($G = 10.02$, $p < 0.025$; $G = 40.13$, $p < 0.001$; $G = 9.86$, $p < 0.025$, respectively, each test with $df = 3$). Subdividing the data indicates that, in each of these cases, female feeding behaviour differed from that of males, with fewer stomachs containing crabs and tunicates but more containing mysids.

To investigate the relationship between non-cephalopod and cephalopod prey, the occurrence of non-cephalopod prey in stomachs with or without whole squid remains (i.e. something other than squid beaks) was examined. For fish in a whole or semi-digested condition (not just skeletal remains), the presence in males was dependent on the presence of squid, with fish being more prevalent in stomachs containing cephalopods ($G = 12.11$, $p < 0.001$, $df = 1$), whereas for females it was independent of the presence or absence of squid ($G = 2.10$, $p > 0.1$, $df = 1$). For tunicates and mysids, their presence in male or female sperm whales was independent of the presence or absence of squid ($G = 0.61$, $p > 0.25$ [males], $G = 0.57$, $p > 0.25$ [females] for tunicates; $G = 0.003$, $p > 0.95$ [males], $G = 1.31$, $p > 0.25$ [females] for mysids). There were too few occurrences of crabs in the stomachs for any quantitative comparison. Although these results are partly dependent upon the relative rates of digestion of cephalopod and non-cephalopod prey, they suggest that (apart from males feeding on fish) the consumption of non-cephalopod prey represents neither "accidental" intake during feeding on cephalopods nor the independent utilization of an alternative resource to cephalopods. They can be considered rather as secondary prey items, exploited during normal foraging dives. The apparent dependence of fish in male stomach contents with the presence of squid is difficult to explain at this stage.

CEPHALOPODS

Because of the difficulties encountered in identifying cephalopods from sperm whale stomachs in the flesh (see above), and because different species are likely to be digested at different rates, the most accurate determination of the ratios between cephalopod prey species of sperm whales probably comes from identifications based on lower beaks (Clarke 1980). However, such analyses have disadvantages. A few beaks cannot be identified to species and have to be assigned to a genus or species group. Some of the smaller squid species may represent secondary prey items of larger squid, and so are not true prey items for the whale. Last, because squid beaks tend to accumulate in sperm whale stomachs, there is the possibility that migrating whales can introduce "alien"(or non-endemic) cephalopods into the region.

Clarke (1980, Table V) identified more than 31 taxa of cephalopods from beaks collected at Donkergat in 1963. Some 24 of these species were common to both sexes and all male size groups, and 26 were common to all groups, except for large males.

In Figure 2, the most commonly occurring cephalopods in sperm whale stomachs at Donkergat are expressed as percentages of the total number and mass eaten. Numerically, 11 species or species groups (*Histioteuthis* A1, A2 + 3, and B, *Teuthowenia megalops*, *Octopoteuthis rugosa*, *Pholidoteuthis boschmai*, *Moroteuthis robsoni*, *Ancistrocheirus lesueuri*, *Phasmatopsis* sp., *Taonius pavo* and *Taningia danae*) each constituted >1% of all cephalopods eaten by female and small male sperm whales, and together made up at least 93% of all cephalopods eaten by those groups (Fig. 2a). Females seemed to consume relatively more histioteuthids and small males relatively more *P. boschmai*, *M. robsoni* and *A. lesueuri*, but other-

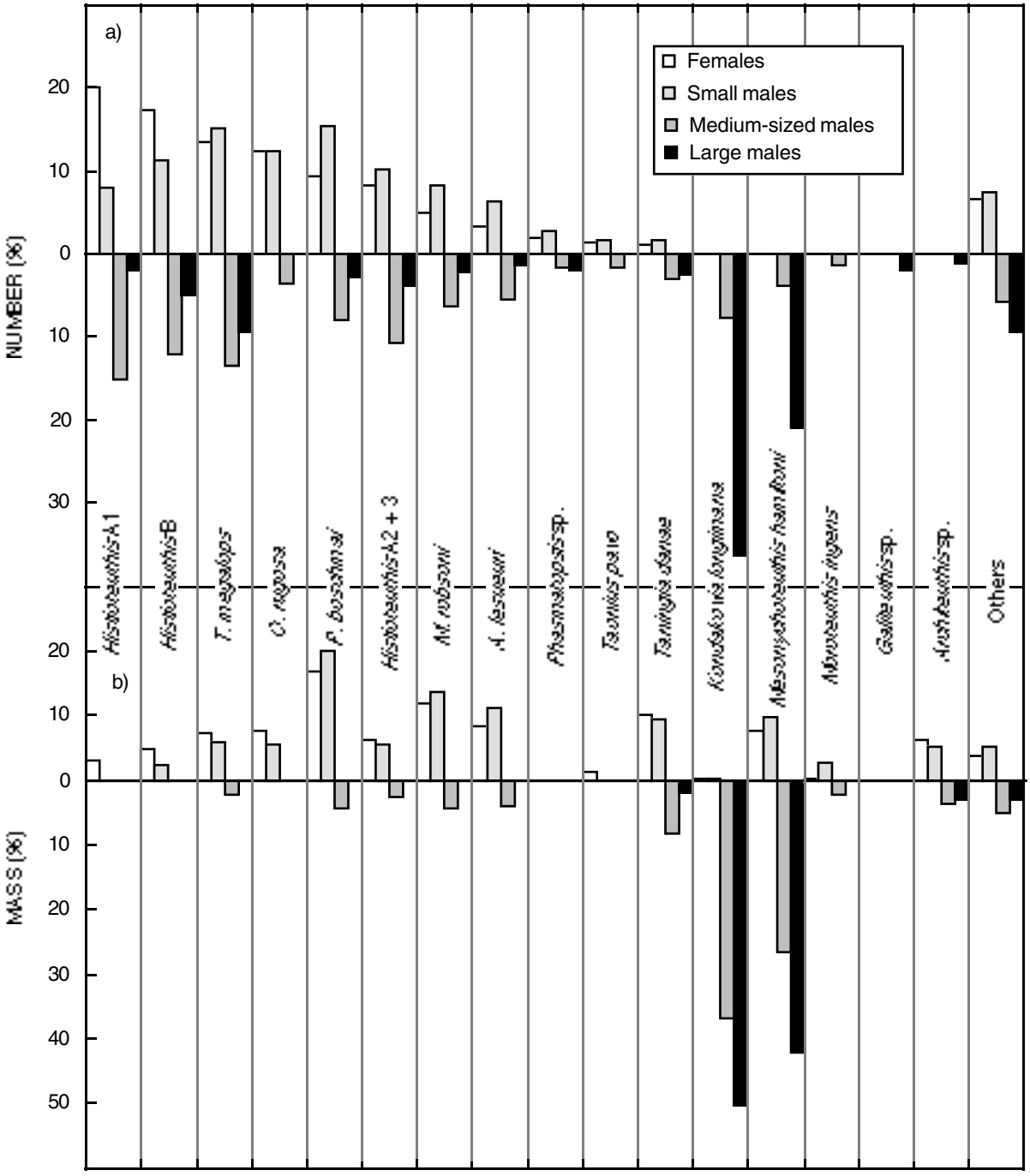

Fig. 2: Incidence of the most important cephalopod species, (a) by number and (b) by mass, in the stomachs of (top) female and small male and (bottom) medium-sized and large male sperm whales examined at Donkergat, 1962–1963 on beak analysis in Clarke 1980)

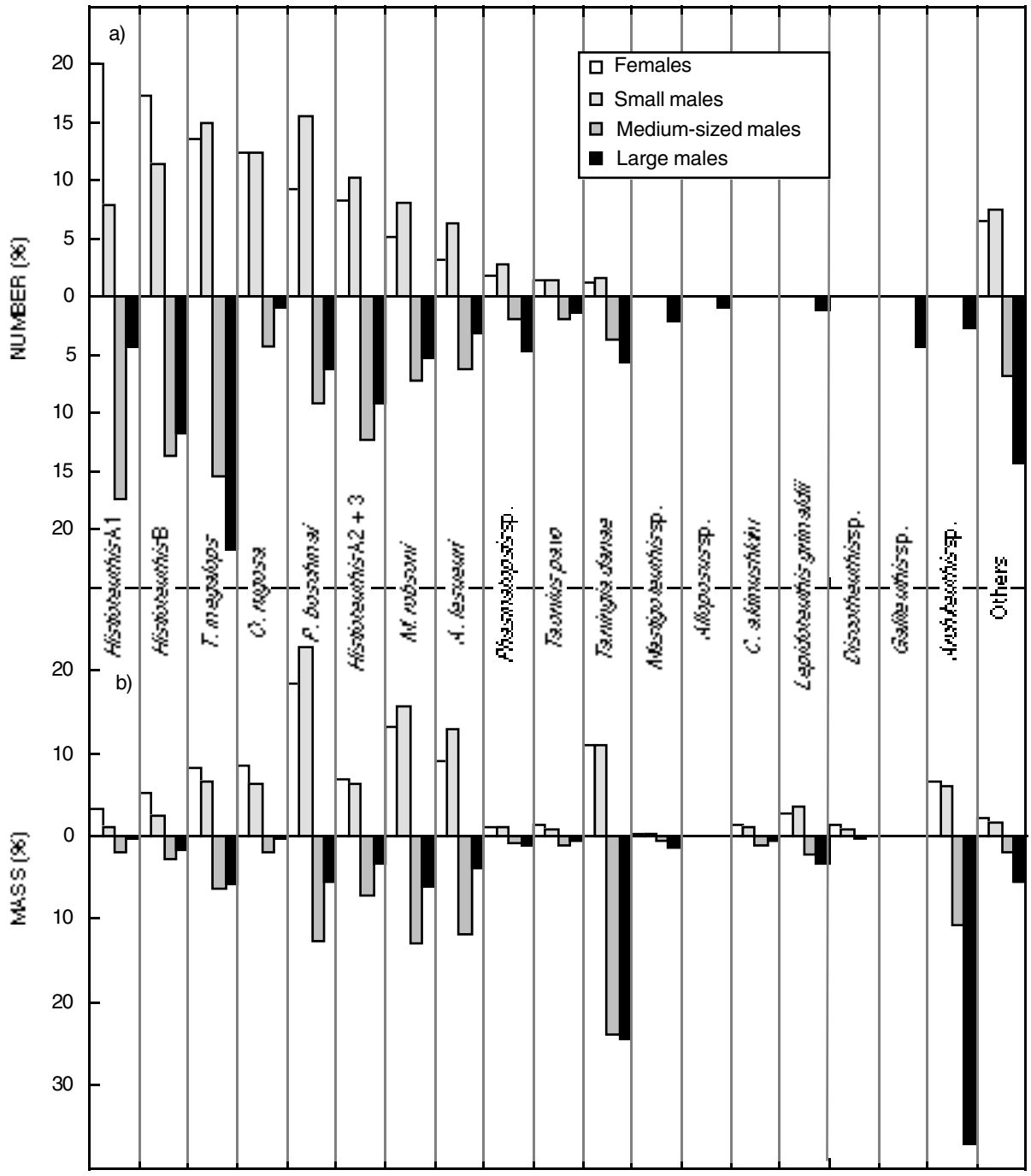

Fig. 3: Incidence of the most important cephalopod species (excluding non-endemics), (a) by number and (b) by mass, in the stomachs of (top) female and small male and (bottom) medium-sized and large male sperm whales examined at Donkergat, 1962–1963 (from Clarke 1980)

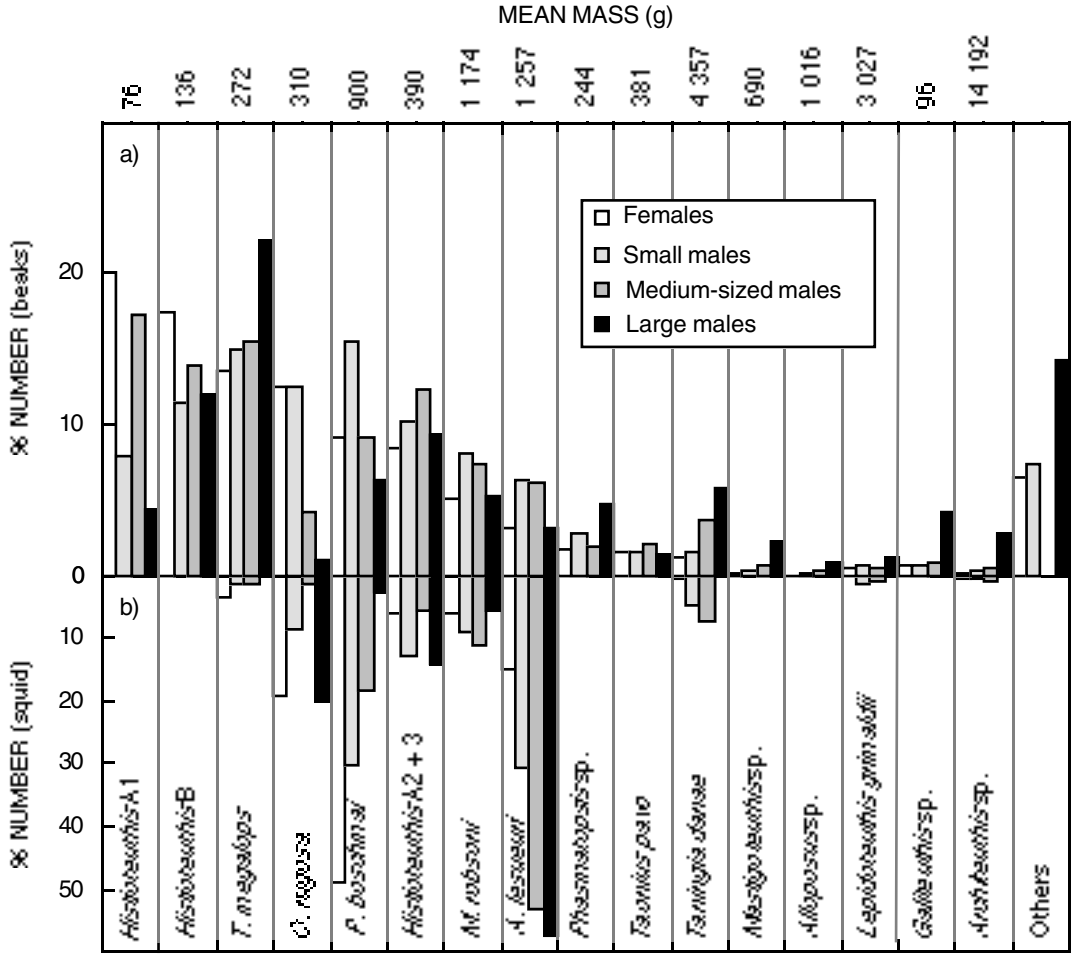

Fig. 4: A comparison of the numerical incidence of cephalopod species in sperm whale stomachs examined at Donkergat, 1962–1963, as determined from (top) squid beak analysis (after Clarke 1980) and (bottom) field identification of the mantles (mean mass of each species as determined from squid beak analysis is shown on the top axis)

wise the species breakdowns were similar. Medium-sized and large males consumed the same 11 "species", but to a lesser extent (81 and 31% respectively), and there seemed to be considerably fewer *O. rugosa*, but more *Taningia danae*, eaten. However, the biggest differences were in the increased proportions of *Kondakovia longimana*, *Mesonychoteuthis hamiltoni*, and (to a lesser extent) *Moroteuthis ingens*, *Galiteuthis* sp. and *Architeuthis* sp., eaten by medium-sized and especially large males.

This picture changed when the contribution of each species was expressed in terms of mass rather than number (Fig. 2b). The 11 most important species by number only constituted 76 and 79% of the total mass consumed by small males and females respectively, and apart from a decline in importance of histioteuthids to both small males and females, *P. boschmai* became the most important species to both groups. Other large squids that had accounted for <1% by number for females and small males now became important components of the diet: these included *M. hamiltoni*, *Moroteuthis ingens* and *Architeuthis* sp. For medium-sized, and especially large males, the change was more dramatic, with the two large squids *K. longimana* and *M. hamiltoni* now constituting 63 and 92% respectively by mass of all the cephalopods

Table VI: Frequency of occurrence (*FO*) and numbers of different squid types, as identified by the author in sperm whale stomach contents at Donkergat, 1962 – 1963

Code name (species)	Small males		Medium males		Large males		Females		Total	
	FO	*n*	*FO*	*n*	*FO*	*n*	*FO*	*n*	*FO*	*n*
Dumpy (*Ancistrocheirus lesueuri*)	149	506	47	237	8	20	41	101	245	864
Chequered (*Pholidoteuthis boschmai*)	111	500	27	82	2	1	80	334	220	916
Purple small fin (*Histioteuthis miranda*)	61	214	15	24	2	5	23	35	101	278
Histioteuthid (*Histioteuthis bonnellii*)	8	12	3	2	0	0	6	6	17	20
Spotted heart fin (*Moroteuthis robsoni*)	67	148	14	49	2	2	24	40	107	239
Tiny (*Octopoteuthis rugosa*)	59	145	5	6	2	7	39	131	105	289
Scaly (*Lepidoteuthis grimaldii*)	8	21	3	4	0	0	0	0	11	25
Architeuthis (*Architeuthis* sp.)	7	7	4	4	0	0	4	5	15	16
Cucioteuthid (*Taningia danae*) + Bat-wing	17	82	13	33	0	0	4	5	34	120
Bugle, large head (*Cycloteuthis akimushkini*)	2		1		0		1		4	
Long white thin (*Teuthowenia megalops*?)*	13	23	5	6	0	0	11	25	29	54
Total		1 658		447		35		682		2 822

* May also include other cranchiids (*Taonius pavo*, *Galiteuthis* sp., *Phasmatopsis* sp.)

eaten.

This suggests that medium-sized and large males preferentially eat larger species of squid than females or small males. However, Clarke (1980) points out that at least four of the species of cephalopod whose beaks were found in sperm whales at Donkergat (*K. longimana*, *M. hamiltoni*, *M. ingens* and *Gonatus antarcticus*) are believed to be confined to Antarctic or sub-Antarctic waters. To these can be added *Alluroteuthis antarcticus* (M. R. Clarke, pers. comm.). Sperm whales (like some other marine mammals) are believed to retain beaks in the stomach for between 1.2 and 2.5 (and up to 10) days (Clarke 1980), and a retention time of up to 33 h has been demonstrated experimentally in northern fur seals (Bigg and Fawcett 1985). The presence of beaks from Antarctic or subAntarctic cephalopods in sperm whale stomachs at Donkergat therefore presumably resulted from the recent immigration of these whales from farther south. This conclusion is supported by the fact that, despite their size, no flesh remains of these squid species (even buccal masses) were found in stomachs at Donkergat. As Clarke (1980) concluded, these species should be considered as "aliens" (non-endemic) in the diet of sperm whales in the region.

The species composition of cephalopods eaten by sperm whales at Donkergat has therefore been reanalysed from the beak data, omitting the five non-endemic species (Figs 3a, b). There is little change to the diet of females and small males, because the non-endemic species were not well represented in their stomach contents. However, there are marked differences in the diet of medium-sized and particularly large males. Numerically, their diet is now closer in composition to that of females and small males, with the principal 11 species eaten by females and small males forming 93 and 74% of those eaten by medium-sized and large males respectively. However, on a mass-based analysis, the differences in the diet of medium-sized and especially large males reappear. This is mainly because of the preponderance of *Taningia danae* in their diet and, in the case of large males, to the consumption of *Architeuthis* sp., which constituted 37% of the diet by mass.

The evidence from squid beaks therefore suggests that, as found for sperm whales killed off Durban (Clarke 1980), medium-sized and particularly large male sperm whales at Donkergat may have fed more frequently on larger species of squid than females or small males, even after allowing for non-endemic cephalopod species present in their stomach contents.

The value of the evidence from whole squid in the stomachs is dependent on the accuracy with which the author was able to allocate them to species correctly, and so must remain uncertain. Nevertheless, 2 822 specimens, attributable to 11 different nominal species, could be recognized, including seven of the commoner species or species groups eaten by females and small males, plus a few other distinctive forms, such as *Architeuthis* sp. (Table VI). A comparison of the numerical incidence of these with the proportions of the 11 commoner endemic species (plus *Architeuthis* sp.) as determined from squid beaks is given in Figure 4, along with the mean mass of each species consumed as determined from the beaks. This shows that no whole specimens attributable to two of the smallest species (*Histioteuthis* A1 and B, with a mean mass of 76 and 136 g respectively) were found. In addition, all

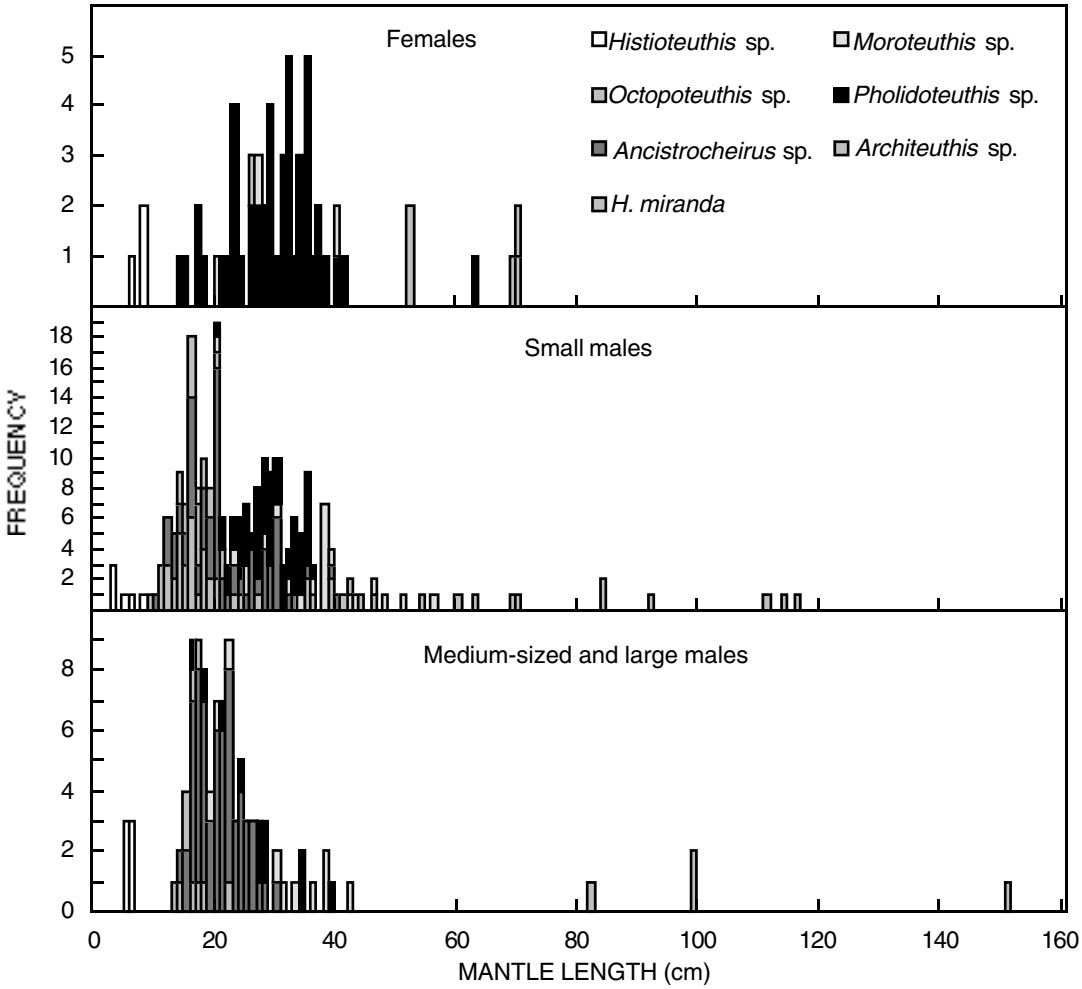

Fig. 5: Size (mantle length) composition of cephalopods eaten by female, small male, and medium-sized plus large male sperm whales at Donkergat, 1962–1963

cranchiid squids, which have thin-walled or gelatinous bodies that are quickly digested (Clarke 1980), were either completely unrepresented as whole squid (*Phasmatopsis* sp., *Galiteuthis* sp., *T. pavo*) or very much under-represented (*T. megalops*). For the remaining species, with mean mass ranging from 310 to 14 192 g, reasonable numbers of whole squid were found, with the exception of *Mastigoteuthis* sp., which formed 0.6% or less of the beaks identified, except in large males. Unfortunately, too few whole squid (n = 35) were recorded from the stomachs of large males to make a credible comparison with other groupings, so that the lack of any recorded *Taningia danae* or *Architeuthis* sp. specimens in large males, for instance, cannot be taken as meaningful. Nevertheless, the whole squid data do indicate that medium-sized males took higher proportions of the larger squid species (*Architeuthis* sp., *Taningia danae*, *Ancistrocheirus* sp. and *M. robsoni*) than either small males or females, and that females took higher proportions of the smaller squid species (*T. megalops*, *O. rugosa* and *P. boschmai*) than either small or medium-sized males.

Individual mantle length data from squids measured in the field are shown in Figure 5. Only four squid from large males were measured, so the data for large and medium-sized males have been combined. Although

Table VII: Non-cephalopod prey items identified from sperm whale stomach contents at Donkergat, 1962 and 1963

Whale number	Date	Length (m)	Sex	Species
			Fish	
34	30 Jul. 1962	9.4	M	*Ruvettus pretiosus*
330	12 Sep. 1962	10.7	M	?*Ceratias holboelli*
400	24 Sep. 1962	15.8	M	*Bathyraja smithii*
407	24 Sep. 1962	12.8	M	*Lophius vomerinus* + 2 fragments of skate
426	25 Sep. 1962	10.7	F	*Ruvettus pretiosus*
613	10 Oct. 1962	13.4	M	?*Ceratias holboelli*
627	11 Oct. 1962	13.1	M	*C. holboelli*
730	23 Oct. 1962	12.5	M	Probably scombrid remains
744	25 Oct. 1962	10.4	F	*Ruvettus pretiosus*
772	29 Oct. 1962	12.8	M	*Cryptopsaras couesii*
774	29 Oct. 1962	11.0	M	*Alepisaurus ferox*
796	31 Oct. 1962	11.9	M	*Ceratias holboelli*
1006	2 Mar. 1963	10.4	F	*Scomberesox saurus*
1038	7 Mar. 1963	10.7	F	*Ceratias holboelli*
1040	7 Mar. 1963	11.0	F	*C. holboelli*
1069	20 Mar. 1963	11.0	M	?*Cryptosaras couesii*
1081	22 Mar. 1963	10.4	M	*C. couesii*
1095	22 Mar. 1963	10.4	M	*Alepisaurus ferox*
1105	22 Mar. 1963	12.8	M	Ceratid anglerfish
1204	18 Apr. 1963	13.1	M	*Ceratias holboelli*
1226	23 Apr. 1963	11.9	M	Ceratid cf *Ceratias holboelli*
1287	8 May 1963	12.5	M	*Ceratias holboelli*
1321	9 May 1963	10.4	F	*Ruvettus pretiosus*
1595	18 Jun. 1963	10.7	F	*R. pretiosus*
1629	20 Jun. 1963	10.0	F	*R. pretiosus*
1731	17 Jul. 1963	11.6	M	Cf *Lophius vomerinus* + egg cases of *Rajella barnardi* and *Cruriraja parcomaculata*
1732	17 Jul. 1963	11.9	M	Zeid *cf Allocyttus verrucosus*
1734	17 Jul. 1963	11.3	M	Cf *Lophius vomerinus*
1735	17 Jul. 1963	11.9	M	*Merluccius capensis**
1736	17 Jul. 1963	11.9	M	Ceratid angler fish
1737	17 Jul. 1963	11.6	M	Ceratid cf *Ceratias holboelli*
1816	6 Aug. 1963	10.4	F	*C. holboelli*
2643	23 Oct. 1963	12.2	M	Cf *Genypterus capensis*
			Crustaceans (crabs)	
349	14 Sep. 1962	10.4	M	*Geryon quinquedens*†
400	25 Sep. 1962	15.8	M	*G. quinquedens*†
432	26 Sep. 1962	11.3	M	Legs of *Neolithodes ?capensis*
626	12 Oct. 1962	12.8	M	*G. quinquedens* (×2)†
1729	17 Jul. 1963	11.6	M	*G. quinquedens*†
1731	17 Jul. 1963	11.6	M	*G. quinquedens*†
1732	17 Jul. 1963	11.9	M	*G. quinquedens*†
			Crustaceans (mysids)	
643	13 Oct. 1962	11.6	M	*Sergestes* cf *regalis*
1052	16 Mar. 1963	10.0	M	*Gnathophausia ingens*
1720	12 Jul. 1963	10.0	F	*G. ingens*
1731	17 Jul. 1963	11.6	M	*Sergestes ?phorcus*
1734	17 Jul. 1963	11.3	M	*S. phorcus*
			Tunicates	
137	14 Aug. 1962	11.9	M	*Pyrosoma atlanticum*
336	13 Sep. 1962	10.7	M	*P. atlanticum*
437	25 Sep. 1962	12.8	M	*P. atlanticum*
438	25 Sep. 1962	10.0	F	*P. atlanticum*
543	3 Oct. 1962	10.7	M	*P. atlanticum*
550	3 Oct. 1962	11.0	M	*P. atlanticum*

Table VII *(continued)*

Whale no.	Date	Length (m)	Sex	Species
615	10 Oct. 1962	11.9	M	*P. atlanticum*
720	23 Oct. 1962	11.9	M	*P. atlanticum*
732	23 Oct. 1962	12.2	M	*P. atlanticum*
743	25 Oct. 1962	15.2	M	*P. atlanticum*
770	29 Oct. 1962	12.2	M	*P. atlanticum*
774	29 Oct. 1962	11.0	M	*P. atlanticum*
800	1 Nov. 1962	10.4	F	*P. atlanticum*
804	1 Nov. 1962	10.4	M	*P. atlanticum*
1098	22 Mar. 1963	11.9	M	*P. atlanticum*
1107	22 Mar. 1963	13.4	M	*P. atlanticum*
1186	14 Apr. 1963	12.2	M	*P. atlanticum*
1189	14 Apr. 1963	11.3	M	*P. atlanticum*
1220	23 Apr. 1963	12.2	M	*P. atlanticum*
1223	23 Apr.l 1963	12.2	M	*P. atlanticum*
1408	19 May 1963	10.7	M	*P. atlanticum*
1468	28 May 1963	15.2	M	*P. atlanticum*
1907	18 Aug. 1963	10.7	M	*P. atlanticum*
2593	16 Oct. 1963	12.2	M	*P. atlanticum*
2603	16 Oct. 1963	12.8	M	*P. atlanticum*
			Other	
1645	21 June 1963	10.7	M	*Pachyptila desolata*

* Secondary item from fish stomach
† Now considered more likely to have been *G. chuni* or *G. macphersoni*

the largest measured squid was smallest in females (70 cm) and largest in medium-sized males (154 cm), the overall distribution of mantle lengths reflected a decreasing rather than an increasing size of squid from females to medium-sized males. However, apart from small males (n = 234), the sample sizes were small (n = 102 for medium-sized/large males and n = 59 for females), and dominated by different species: 80% of the squid measured from females were identified as *P. boschmai* and 59% of those measured from medium-sized and large males as *A. lesueuri*. Nevertheless, the data show that sperm whales were eating squid with mantle lengths as small as 3 cm, and that the most frequently-consumed size-class in males was around 15–25 cm mantle length.

From the analysis of squid beaks collected at Donkergat, Clarke (1980, Table IX) showed that the mean mass of individuals of a particular cephalopod species eaten by females were more likely (18 of 23 species) to be lower than those eaten by males, particularly medium-sized and large males (1 of 23 species).

FISH

The commonest fish eaten by sperm whales at Donkergat were ceratid angler fish, being identified from material collected from 16 whales (Table VII), and presumed (from gross similarities in the field) to have occurred in another 23 whales. Of the 16 collected specimens, seven were definitely (and four possibly) *Ceratias holboelli* and two definitely (and one possibly) *Cryptosaras couesii*: the remaining two specimens could only be attributed to "ceratid sp." Specimens identified as oilfish *Ruvettus pretiosus* were collected from six whales, and presumed (from gross similarities in the field) to have occurred in another five whales. Skeletal material attributable to rajids was collected from three whales (one of which was identified as *Bathyraja smithii*), but similar material was recorded from another seven whales in the field, in each of which from 1 to 14 egg cases were also found (egg cases in one whale were attributed to *Rajella barnardi* and *Cruriraja parcomaculata*). Material attributable to the longsnout lancetfish *Alepisaurus ferox* was collected from two whales and recorded in the field from another. Monkfish *Lophius vomerinus* were recorded on one (and possibly three) occasions, with a single record of a zeid similar to *Allocyttus verrucosus*, and one possible instance of the consumption of kingklip *Genypterus capensis*. A further 32 whales were recorded with unidentifiable fish remains in the stomach.

The incidence of ceratids among whales eating fish was not significantly different between females,

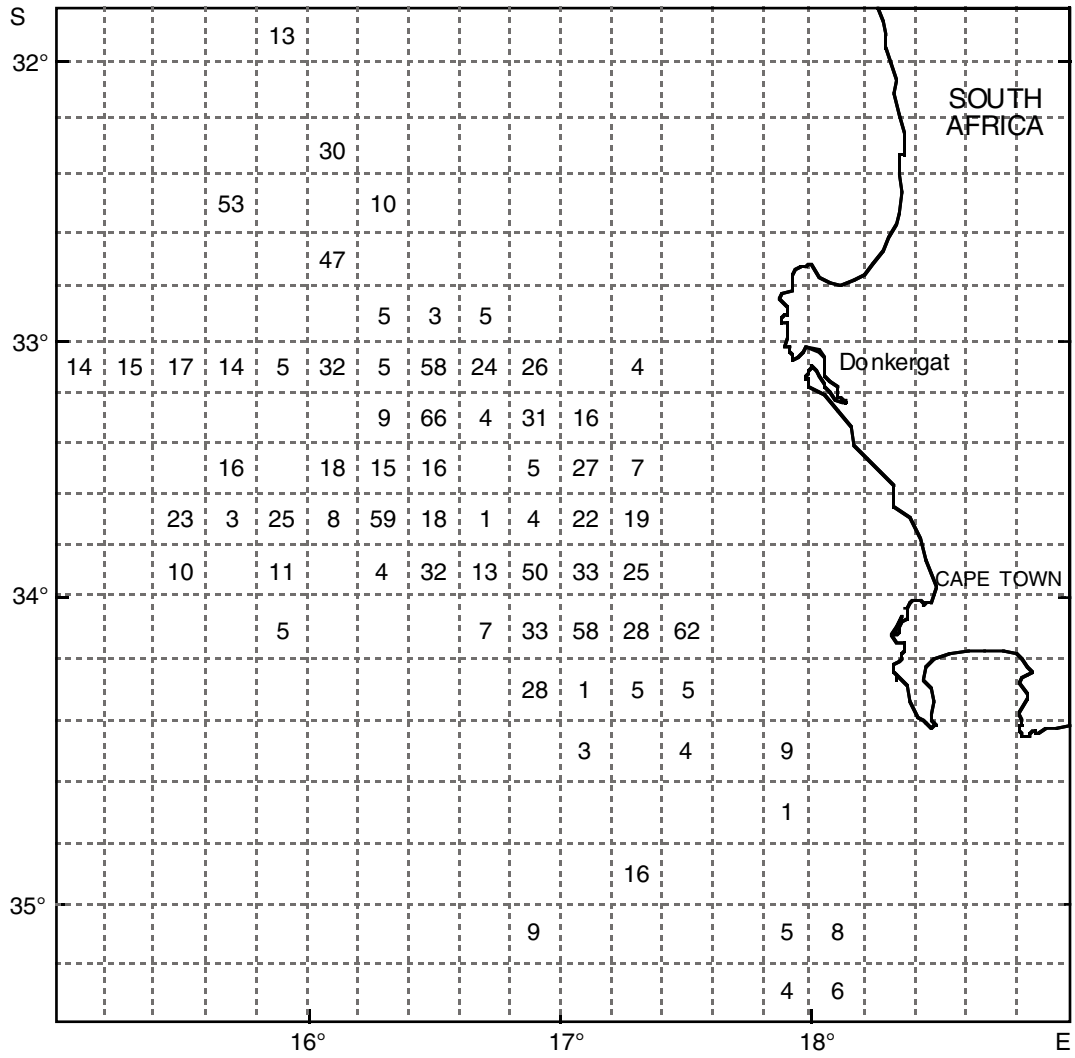

Fig. 6: Catch positions of sperm whales whose stomach contents were examined at Donkergat, 1962–1963. Grid cells c. 22 × 18 km each

small males, and medium-sized and large males combined ($G = 1.93$, $p > 0.25$, $df = 2$). The incidence of *Ruvettus pretiosus*, however, was significantly different between females and all males combined ($G = 19.03$, $p < 0.001$, $df = 1$), being 40.9% in females eating fish and 2.9% in males eating fish. Additionally, there seemed to be a gradation in the incidence of feeding on rajids, with none being found in females, but 10.6% of small males and 23.8% of medium-sized and large males with fish in the stomach feeding on rays. All four whales from which *Lophius vomerinus* was definitely or possibly recorded were males, as were all three whales from which *Alepisaurus ferox* was recorded.

Apart from three small males, whose stomachs contained the skulls of 9, 9 and 10 rajids respectively, all other sperm whales feeding on fish contained the remains of only one (92.4%) or two (7.6%) fish.

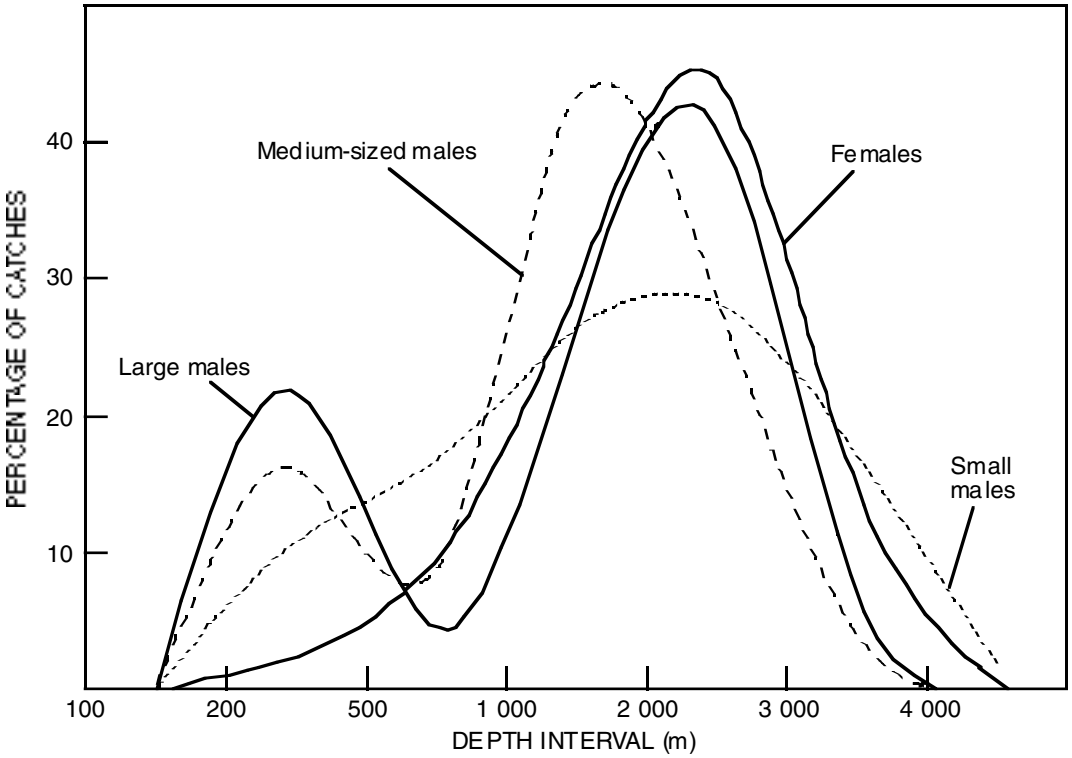

Fig. 7: Multiple spline curves fitted to the distribution of catch positions by depth interval for female, small, medium-sized and large male sperm whales examined at Donkergat, 1962 and 1963

CRUSTACEANS

Crabs were identified to species from seven of the 12 stomachs in which they were found (Table VII). Animals identified as *Geryon quinquedens* (but now considered more likely to have been *G. chuni* or *G. macphersoni*) were found in six whales, and a stone crab *Neolithodes ?capensis* was found in the remaining whale. Numbers of crabs per whale ranged from 1 to 4, with a mean of 1.5. Crabs were only found in the stomachs of male sperm whales.

Decapod crustaceans (mysids or prawns) were recorded from 94 sperm whales. Of these, 88 were described as mysids, and examples collected from two whales both proved to be *Gnathophausia ingens*. The remaining six whales were recorded as feeding on prawns: examples collected from three whales proved to be *Sergestes phorcus* or *S.* cf *regalis* (Table VII). The numbers of mysids recorded per whale varied from 1 to 13, with a mean of 2.4. If the data are grouped into stomachs containing one mysid and those containing two or more, female sperm whales proved to have a greater proportion of stomachs containing more than one mysid than males ($G = 11.11$, $p < 0.001$, $df = 1$). Overall, the mean number of mysids per whale was 2.85 for females and 1.53 for males. The numbers of *Sergestes* prawns found in each whale ranged from 1 to 3, with a mean of 1.33.

TUNICATES

Specimens were collected from 25 of the 73 sperm whales in which tunicates were found (Table VII). All were identified as *Pyrosoma atlanticum* forma *dipleurosoma*. The number of tunicates per stomach ranged from 1 to 6, with a mean of 1.5. If data are grouped into stomachs containing one tunicate and those containing two or more, there is no significant difference between the proportions of these two groups in male and female sperm whales ($G = 0.43$, $p > 0.50$, $df = 1$).

OTHERS

An intact but partly digested prion *Pachyptila desolata* (presumably the Antarctic prion *P. vittata desolata*) was found in the stomach of a 10.7 m male killed on 21 June 1963 (Table VII).

Distribution of whales and food items

The numbers of sperm whales caught per 12-minute cell are shown in Figure 6. They are not expressed in terms of the amount of hunting effort. Therefore, whereas the overall rarity of sperm whales (<10% of catches) in water <500 m deep is probably real (given the frequency with which this stratum must have been traversed by catchers travelling between whaling station and whaling ground), the decline in numbers of whales in deeper waters is probably more reflective of a reduction in catching effort with distance from the whaling station (Best 1969). Catches occurred in water more than 4 000 m deep.

There were obvious differences between the inshore-offshore distributions of catches of female and small, medium and large males (Fig. 7). The relative numbers of whales caught in water shallower or deeper than 1 000 m (inshore/offshore) were not independent of sex and male size-class ($\chi^2 = 32.99$, $p < 0.001$, $df = 3$). For males alone, however, distribution inshore/offshore was independent of size-class ($\chi^2 = 0.57$, $p > 0.75$, $df = 2$). Therefore, a greater proportion of the catches of females seems to have occurred in water deeper than 1 000 m than was the case for any male size-class. In water deeper than 1 000 m, there were also differences in distribution between small, medium and large males and females in the depth intervals 1 000–2 000, 2 000–3 000 and >3 000 m ($\chi^2 = 54.7$, $p < 0.001$, $df = 6$). Only females and large males showed a similar pattern, peaking at depths of between 2 000 and 3 000 m ($\chi^2 = 1.40$, $p > 0.5$, $df = 2$). The offshore distribution of medium-sized males appeared to be skewed towards shallower water than for females and large males, and the offshore distribution of small males toward deeper water.

There seem no clear operational reasons why these patterns should have developed. The increased *per capita* cost of towing a whale from a greater distance offshore would seem to make it more profitable to exploit small males or females closer to the station, although this might be offset by the possibility of catching larger numbers of the smaller size-classes at one time (because they occurred in larger schools).

It therefore appears that, within the West Coast whaling ground, some groups of male sperm whales (particularly medium-sized and large individuals) preferentially visited waters over the upper reaches of the continental slope, in water <1 000 m (and mostly between 200 and 500 m) deep. Beyond 1 000 m, medium-sized males tended to be caught in relatively shallower water, and small males in relatively deeper water, than females or large males.

Among the non-cephalopod prey, there seemed to be a gradation with depth, such that the proportions found in whales taken in water depths of >2 000 m varied from 0% for rays, 8.3% for crabs, 42.5 % for *Pyrosoma* sp., 46.2% for ceratids and 60% for mysids, to 80% for *Ruvettus pretiosus*. (Fig. 8).

DISCUSSION

Time of feeding

The lack of any significant difference in the incidence of food in the morning, midday or afternoon suggests that there may have been no diurnal variation in feeding intensity of either males or females on the West Coast whaling ground. This agrees with the conclusions of Okutani and Nemoto (1964) for the northern part of the North Pacific and Clarke (1980) for various localities, but disagrees with that of Mat-sushita (1955). In the Antarctic, Matsushita (1955) found increased stomach fills early in the morning (03:00–08:00) and evening (22:00–24:00) compared to intervening hours and proposed that sperm whales fed more actively at night than in daytime. This apparent difference could either reflect the greater coverage of the day in Matsushita's data, or a difference in feeding behaviour with locality. Tracking of small sperm whales (9.5–10.9 m) by asdic off Durban, South Africa, suggested that the whales dived deeper and for longer periods as the day progressed, but there were no observations between 20:30 and 04:30 (Lockyer 1977). Data collected from two males tagged with transponders in the South-East Caribbean were inconclusive as regards diel patterns of activity: although afternoon dives were not longer than in the rest of the daylight hours, there were suggestions of dives just after dark being longer than those just before dark (Watkins *et al.* 1993). In addition, on two days of tracking, groups of whales spent hours at the surface during the day and then dived continuously after dark. In female sperm whales off the Galapagos Islands, both visual and acoustic measures of "sociality" rose to a pronounced peak in late afternoon and fell rapidly just before sunset (Whitehead and Weilgart 1991). Trends during darkness (as measured by acoustic activity)

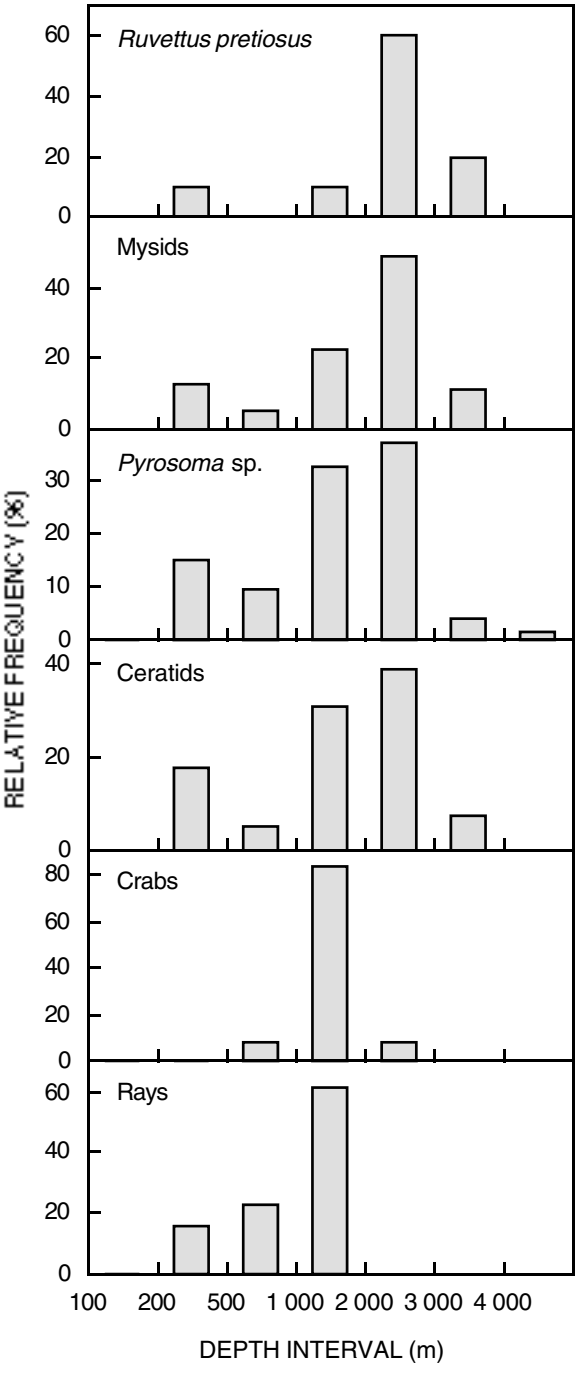

Fig. 8: Relative frequency of non-cephalopod food items with depth interval in the stomachs of sperm whales examined at Donkergat, 1962 and 1963

were less clear. Whitehead and Weilgart (1991) suggested that the predominance of aggregation in late afternoon might correspond to a lowering in feeding success at that time of day, but no relationship between feeding success (as measured by defecation rate) and "sociality" could be found. Overall, visual and acoustic observations indicated that female sperm whales off the Galapagos Islands spent about 75% of the day in foraging, and 25% at or near the surface. Sperm whale stomachs in general are characterized by large accumulations of indigestible prey remains such as cephalopod beaks, which may be characteristic of a species that is a frequent feeder, or "nibbler", rather than a "meal eater" (Jobling and Breiby 1986). Difficulties in detecting diel variation in feeding behaviour may therefore partly reflect this foraging strategy, and partly the difficulty of obtaining data on feeding behaviour after dark.

Diet and feeding habits

In an examination of the contents of some 2 400 sperm whale stomachs from Chile and Peru, only three species of squid were found as flesh remains, of which 99.45% were identified as one species, *Dosidicus gigas* (R. Clarke *et al*. 1988). This finding was in sharp contrast to that of M. Clarke *et al*. (1976), who found no less than 18 cephalopod taxa in samples of beaks taken from stomachs of seven of the above whales; three small cephalopod species in the genera *Histioteuthis*, *Chiroteuthis* and *Ancistrocheirus* constituted 68% of the number of beaks present. R. Clarke *et al*. (1988) concluded that these smaller species were not consumed directly by the sperm whale, but were actually prey items from the stomachs of *Dosidicus gigas*. In response, M. Clarke *et al*. (1993) pointed out that the three small species were all represented by flesh remains, not just beaks: it was their opinion that the differing conclusions may have been the result of different oceanographic conditions in the years of sampling. However M. Clarke *et al*.'s (1976) samples were apparently collected from the same years and localities as R. Clarke *et al*.'s (1988) data, so the discrepancy remains unresolved. At Donkergat, the differences between the species composition of the cephalopods identified in the flesh and from their beaks can be explained fairly readily by the small size (<150 g) and/or thin-walled body structure of the "missing" whole squid. These species were presumably digested too rapidly to leave intact mantles in the stomach by the time the whale was examined on the flensing platform. As four of the species "missing" as whole squid were represented by buccal masses, the alternative explanation (that they were secondary prey items)

seems unlikely.

The stomach content data from sperm whales landed at Donkergat indicate a number of differences between the feeding habits of females and males in the region. These can be summarized as follows:

(i) Medium-sized and large males feed less intensively than small males and females;
(ii) Medium-sized and large males eat more non-endemic species of cephalopods than small males or females;
(iii) Medium-sized and large males feed more frequently on larger species of endemic cephalopods than females or small males;
(iv) Males generally eat larger individuals of a cephalopod species than females (Clarke 1980);
(v) Males in general eat crabs and tunicates more frequently than females;
(vi) Females eat mysids more frequently (and in greater numbers) than males in general;
(vii) Females eat *R. pretiosus* more frequently than males in general;
(viii) Medium-sized and large males feed more frequently than small males on rajids, whereas females have not been recorded as taking them;
(ix) Only males feed on *Lophius vomerinus* and *Alepisaurus ferox*.

In addition, the data from catch positions indicate that relatively few females were caught in water <1 000 m deep compared to males, and that prey items favoured by males (crabs and rajids) were found more often in stomachs of whales taken in water <2 000 m deep. However, prey items favoured by females (mysids, *R. pretiosus*) were mainly found in stomachs of whales taken in water >2 000 m deep.

Other evidence indicates that medium-sized and large males migrate seasonally into the whaling grounds from farther south (Best 1969). Their lower intensity of feeding in the region, and the presence of non-endemic cephalopod species in their stomachs, are therefore probably a consequence of this migration. The other differences, however, cannot be explained on this basis.

In the Gulf of Alaska, Tarasevich (1968) found that small male sperm whales (11.6–13 m) fed more intensively than large male sperm whales (>13 m) on species of cephalopods that preferred warmer water, and that they tended to eat smaller individuals of the same cephalopod species than large males. This was attributed to differing vertical distributions, with younger cephalopods, and those species preferring warmer water, being distributed in the upper layers of the ocean. In the waters of the Aleutian chain, such differences were not apparent between small and large males, which Tarasevich (1968) ascribed to a much deeper thermocline in the region. Clarke (1980) has also attributed the tendency for male sperm whales (especially those >12.2 m long) to feed more frequently on larger species of squid (and, in the Donkergat region, on larger individuals of certain squid species) than females to the vertical distribution of their prey, rather than to any active selection by the whale. Larger sperm whales have also been recorded as eating larger individuals of a cephalopod species in the South-East Pacific (for *D. gigas*) and off the Azores (for *Histioteuthis bonnelli bonnelli*) and attributed to the vertical stratification of the prey (R. Clarke *et al*. 1988, M. Clarke et al. 1993). Ontogenetic descent (in which adults are distributed lower in the water column than juveniles) has been described for several species of squid (e.g. Clarke and Lu 1975, Young 1975). As female sperm whales tend to feed on smaller individuals of most of the squid species eaten than (especially large) males, it is possible that they feed higher in the water column. In addition, the two most important squid species by mass eaten by medium-sized and large males at Donkergat (*Architeuthis* sp. and *Taningia danae*) are said to be among those that go near to or on to the sea floor at some stage of their adult existence (Clarke 1980).

Table VIII summarizes the information available on habitat and depth distributions for non-cephalopod prey items in the region. Because many of the depth data originate from specimens collected by commercial trawlers on the West Coast, which rarely trawl to depths >550 m (R. W. Leslie, Marine & Coastal Management, pers. comm.), they might not be fully representative of the real depth distributions of the species concerned. Nevertheless, the available data show that those species "favoured" by females (*R. pretiosus* and mysid prawns) are mesopelagic in habit, whereas those "favoured" by males (rajids and crabs) are more bathypelagic (if not benthic) in habit. Two of the other species only eaten occasionally by males (*L. vomerinus*, *Allocyttus verrucosus*) are also either benthic or mesopelagic (but occurring in shoals close to the bottom) respectively. Ceratids, which were eaten equally by males and females, are believed to be mesopelagic in habitat: Pietsch (1986) report the juveniles and adults as "deep mesopelagic to bathy-pelagic". The evidence from tunicates (seemingly preferred by males) is difficult to evaluate. Metcalf and Hopkins (1932) give information on the depths at which 26 specimens of *Pyrosoma* were collected in the North Atlantic and North and South Pacific oceans. These range from the surface to 1 375 m, with a mean of 353 ± 376 m. Because of this wide range in depths, and the absence of any local data, it is impossible to speculate on why there should be a higher incidence of tunicates in males.

As was the case at Donkergat, crabs *Lithodes antarcticus* and *Paralomis verrucosus* were only found in the stomachs of male sperm whales (1.16% of 1 123 ex-

Table VIII: Depth range and habitats of non-cephalopod prey items of sperm whales off the west coast of South Africa

Species	*n*	Depth		Habitat	Source
		Range (m)	Mean (m)		
			Fish		
Ruvettus pretiosus	6	350 – 549	438	Mesopelagic	South African Museum (SAM) files
Ceratias sp.	6	350 – 945	776	Mesopelagic	"
Cryptosaras couesii	6	585 – 978	747	Mesopelagic	"
Alepisaurus ferox	13	900 – 1 126	1 069	Mesopelagic	"
Allocyttus verrucosus	18	549 – 1 628[3]	870	Mesopelagic, close to seabed	"
Bathyraja smithii	39	440 – 923	691	Benthic	Compagno *et al*. (1991)
Crurirajа parcomaculata	84	170 – 520	305	Benthic	"
Rajella barnardi	68	250 – 923	493	Benthic	"
Lophius vomerinus	–	21 – 814	–	Benthic	R. W. Leslie, MCM, pers. comm.
			Crustaceans		
Sergestes spp.	15	250 – 1 120	614	Mesopelagic?	South African Museum files
Gnathophausia ingens	9	484 – 1 600	894	Mesopelagic?	"
Geryon spp.	15	293 – 1 394[1]	597	Benthic	"
Neolithodes capensis	2	2 688 – 3 268[2]	2 978	Benthic	"

[1] 230 – 1 520 m (Kensley 1981)
[2] 1 000 – 3 000 m (Kensley 1981)
[3] Caught commercially between 600 and 1 000 m

amined) in the South-East Pacific, but not in the stomachs of 784 females examined (Clarke *et al.* 1988).

On balance, the evidence from catch positions and the incidence of non-cephalopod prey items suggests that some males tended to move onto the continental slope (water 200–1 000 m deep) within the West Coast whaling ground, where they dived to the sea floor and took benthic organisms such as rajids, crabs, *L. vomerinus* and *A. verrucosus.* Females stayed farther offshore. Offshore, both males and females fed mesopelagically, consuming mesopelagic-bathypelagic cephalopods, *R. pretiosus*, mysids and ceratids. Evidence from the size of squid eaten suggests that males might feed deeper than females. Given the general paucity of accurate information on prey depth distribution, it is difficult to place quantitative limits on how this feeding might be stratified. The presence of *Neolithodes* sp. remains in the stomach of a male would indicate feeding to a depth of at least 1 000 m, whereas the presence of *Gnathophausia* sp. in the stomachs of females would suggest that this sex must dive to at least 500 m.

Dive depth

According to reports of nineteenth-century open-boat whalers (reviewed by Caldwell *et al*. 1966), female and young male sperm whales took out only about 554 m of line when harpooned, compared to 1 108 m of line for bulls, and the whalers were apparently convinced that females do not dive as deep as large males. Direct tracking of submerged sperm whales by asdic during chasing by a whale-catcher for tagging purposes, however, failed to reveal any significant difference in average dive depths for all sizes of whale, with the mean depths ranging from 315 to 360 m (Lockyer 1977). However, very few (6.5%) sexually mature females and pubertal males, and no immature males and females, or calves and adolescents, dived below 700 m, compared to 16.9% of maturing males (11.0–11.9 m) and 14.6% of mature males: the deepest dive (to 1 140 m) was made by a 13.8 m male. Similarly collected data on dive profiles obtained from a whale-catcher during commercial whaling operations indicated maximum depths of 210–530 m (average = 326 m) for five females and two small males, and 470–570 m (average = 513 m) for two medium-sized and one large male sperm whale (Mano 1986). These maximum depths are significantly different, although the sample sizes are very small (Mann-Whitney Rank Sum Test, $t = -2.466$, $p = 0.039$, $df = 8$). Sperm whale schools consisting mainly of females and their young were tracked by depth-sounder from a yacht in water depths of 2 000–4 000 m off the Galapagos Islands. Maximum depths reached during 48 dives ranged between 250 and 450 m (Papastavrou *et al*. 1989), similar to that apparently observed in deep water off Sri Lanka

(300–600 m, Gordon 1987 as quoted in Whitehead *et al.* 1992). Similar tracking of male sperm whales on the Scotian Shelf revealed dives to depths of 215–415 m, but in water only 275–550 m deep, and 50% of the recorded dives reached the estimated depth of the sea floor; Whitehead *et al.* (1992) concluded that the whales were feeding regularly on or near the bottom. Two sperm whales tagged with acoustic transponder tags were tracked by sonar in the South-East Caribbean; both were believed to be males, from their size (11 and 15 m) and their behaviour (Watkins *et al.* 1993). Both whales dived to depths of 400–600 m and greater, with maximum depths reached being 1 185 m for the 11-m whale and possibly 2 035 m for the 15-m whale (shortly after tagging). Although the bathymetry of the area was not known in detail (highly irregular bottom topography), charted water depths in all cases were approximately the depth of the deeper whale dives.

The results of such tracking studies can be supplemented with more indirect evidence. Clarke (1976) recorded an incidental observation of a sperm whale believed (from its stomach contents) to have dived to the sea floor at a depth of about 3 193 m: although not stated, the whale involved (Platform no. 1979) was a large male 14.3 m long. Roe (1969) recorded a very high incidence of benthic fish species in sperm whales off Iceland; the whales concerned (all large males) were caught in water depths of 500–2 000 m, and the author concluded that they must have been feeding on or near the bottom in depths of at least 500 m. A 14-m male sperm whale was also brought up entangled in an undersea cable on the sea floor from a depth of 988 m (Heezen 1957).

Overall, these data suggest that females and immatures of both sexes rarely dive deeper than about 700 m, whereas pubertal and adult males can dive to depths of 1 000–2 000 m and possibly more. Such deep dives by males seem to be frequently associated with visits to the sea floor. Occasionally, sperm whales may make short-term excursions onto the continental shelf into water as shallow as 41–68 m, presumably to take advantage of locally abundant prey (Scott and Sadove 1997).

Some of the differences in feeding observed between male and female sperm whales may reflect adaptations to their social organization. For example, feeding at a higher level in the water column may be more advantageous for mixed schools (consisting of females and their dependent young) than for schools not containing calves. It has been suggested that there may be communal raising of young within such schools, including "baby-sitting" of juveniles at or near the surface when other members of the school made deep foraging dives (Best 1979, Best *et al.* 1984). Whitehead (1996) has proposed that such baby-sitting may be a form of alloparental care. Feeding higher in the water column would shorten the periods when the school had to be segregated in this manner, and this would in turn presumably reduce the risks (e.g. predation) associated with fragmentation of the school. It is unclear why schools of females and their young would avoid visiting the continental slope to feed on its associated benthic fauna. Perhaps the density or availability of this fauna is such that it tends to provide an energetic advantage for the smaller schools of medium-sized or large males, but not for the bigger schools of cows and their offspring. The near-shore environment might also contain greater risks of predation on young calves from sharks such as great whites *Carcharodon carcharias*, or killer whales *Orcinus orca*. Alternatively, the distribution of sperm whale catches observed in 1962/63 may have been the result of previous exploitation, in which the mixed schools that historically included the continental slope in their home range were eradicated first, as they occurred closest to the whaling station. If female sperm whales have smaller "home ranges" than male sperm whales (Best 1979), and if they show a degree of site fidelity to such ranges (Gordon 1987), then such an effect could well be possible.

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